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NUCLEAR PHENOMENA OF SEXUAL REPRODUCTION IN ALGÆ[1]

DR. BRADLEY MOORE DAVIS
CAMBRIDGE, MASS.

CYTOLOGICAL investigations among the algæ upon the processes of gametogenesis and the developments that follow upon the fusion of gametes have not been numerous and are all of comparatively recent date. The difficulties of obtaining and handling material in critical stages require great patience, but the importance of the problems has attracted attention to a field of enquiry in which considerable progress has already been made and which offers some of the most attractive problems for cytological investigation. There has been a very marked advance in our understanding of the Rhodophyceæ and Phæophyceæ, but the Chlorophyceæ have so far received little attention.

The advance has been chiefly in our interpretation of certain life histories in which complex developments follow upon the phase of sexual reproduction. The publication in 1894 of Strasburger's paper on "The Periodic Reduction of the Number of Chromosomes in the Life History of Living Organisms"[2] marked the beginning of that closer analysis of the life histories of the higher plants which presents the strongest support for the theory of antithetic alternation of generations. The higher plants were naturally the first which were subjected to critical cytological investigation and the structure and behavior of the nuclei through various stages of ontogeny have been studied in an increasing number of forms representative of the most important groups. Later came the pioneer work of this character upon the thallophytes which has given such rich returns in our appreciation of the significance of the critical stages in the complex life histories of certain types of the Ascomycetes, Uredineæ, Phæophyceæ and Rhodophyceæ.

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[1] A paper read by invitation before the Botanical Society of America, Boston, December 30, 1909.

[2] *Ann. of Bot.*, Vol. VIII, p. 281, 1894.

It is the writer's part in this symposium to outline the advances that have been made in cytological research on the sexual reproduction of the algæ, and such enquiry, for a number of reasons, necessarily leads at once to the consideration of life histories with reference to cytological detail. From studies upon the bryophytes, pteridophytes and spermatophytes we have learned that in these groups every sexual nuclear fusion marks the beginning of a distinct phase in the life history, the sporophyte, the nuclei of which carry the double, or diploid, number of chromosomes characteristic of the species. Furthermore, we know that the sporophytic phase comes to an end with the numerical reduction of the chromosomes to the original, or haploid, number peculiar to the gametophyte. This significant period of chromosome reduction is associated in the bryophytes and pteridophytes with the formation of spores, in the spermatophytes with the formation of pollen grains and embryo sacs. Every sexual fusion, then, carries with it a prospective period of chromosome reduction.

Since such is the history for the higher plants we have every reason to expect that each sexual nuclear fusion among the thallophytes with the resulting doubling of the chromatin content in the zygote would be followed sooner or later by reduction phenomena. It becomes a matter of importance to determine when the latter event occurs, since between the time when the gametes fuse and that of chromosome reduction there is always the possibility of an intercalated sporophytic phase in the life history, the development of which will involve the mitoses of nuclei that carry twice the number of chromosomes characteristic of the sexual plant. From this point of view let us then consider in the order of the Chlorophyceæ, Phæophyceæ and Rhodophyceæ some of the recent cytological research which has made much clearer the significance of the life histories of certain important types.

There are in the life histories of a number of the green algæ certain outward signs that would lead one to suspect that the period of chromosome reduction in these forms takes place just previous to or during the germination of the zygospores or oospores. Thus the formation of several zoospores within the zygote of *Ulothrix* and *Hydrodictyon,* and of four zoospores in the oospore of *Œdogonium* at once excites suspicion that the first mitosis in these sexually formed cells is a reduction division. Still more striking is the phenomena described in the zygospores of the Conjugales where the fusion nucleus by two mitoses gives rise to four daughter nuclei, three of which in *Spirogyra* and two of which in the desmids *Closterium* and *Cosmarium* break down. Such behavior, involving a sacrifice of protoplasmic structure and energy, is not easily understood except that it be related to important events of ontogeny and phylogeny. Any one familiar with the cytology of spore formation in the higher plants or with oogenesis in animals would at once suspect that the zygospore of the Conjugales was the seat of reduction phenomena.

That this is really true has been shown by recent work of Karsten[3] who has followed the chromosomes of *Spirogyra jugalis* through the two mitoses within the zygospore. Karsten in agreement with Berghs reached the conclusion that the chromosomes in the resting nucleus of *Spirogyra* lie in the substance of the large nucleole.[4] He was able by the proper extraction of stain to differentiate fourteen bodies in the gamete nucleus which corresponded in number to the fourteen chromosomes that may be readily counted for this species in later mitoses. The union of the gamete nuclei in the zygospore involves the fusion of the two nucleoles to form a dense homogeneous structure in preparation for a characteristic association of the two sets of chromosomes, one derived from each parent.

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[3] Karsten, G., 1908, "Die Entwicklung der Zygoten von *Spirogyra jugalis* Ktzg.," *Flora,* Vol. XCIX, p. 1, 1908.

The approach of the first mitosis is indicated by changes within the fusion nucleole where a granular structure begins to appear, accompanied by irregularities in its form. As these changes proceed an assemblage of deeply staining bodies becomes evident which in later stages are readily identified as chromosomes. There are twenty-eight of these grouped in fourteen pairs, an arrangement which is characteristic of a phase of chromosome reduction that follows synapsis and which signifies that the chromosomes are to be distributed in two sets of equal numbers by the following mitosis. This distribution occurs in *Spirogyra* and the second mitosis in the zygospore is concerned with the reduced, or haploid, number of chromosomes. Thus the double, or diploid, number is present only in the fusion nucleus; the numerical reduction takes place with the first mitosis. There are no nuclear divisions in which the diploid number of chromosomes is passed on, and assuming that the sporophyte generation is characterized by nuclear divisions with the diploid number of chromosomes, there is no sporophytic phase in this life history.

So close is the parallelism between the events of reduction in *Spirogyra* and those of higher plants that Karsten even reports evidence for the premature division of the chromosomes during the first mitosis in preparation for the second division, a phenomenon very characteristic of the reduction divisions of higher plants. The degeneration of three of the four nuclei which result from the two mitoses within the zygospore of *Spirogyra* is of course an illustration of that conservation of material for a single reproductive cell which finds its analogy in the history of development of certain megaspores at the expense of their neighbors and in the maturation of the animal egg.

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[4] B. F. Lutman has, however, recently reported (*Science*, Vol. XXXI, p. 633, 1910) that the chromosomes of *Closterium* are formed from a spirem which has its origin in the fine reticulum around the nucleole.

It seems probable that studies upon the germinating zygospores and oospores of other green algæ will establish them to be the seat of reduction phenomena similar to that described above, although such investigations are beset with many technical difficulties. It is to be hoped that we may soon have information on these conditions in such types as *Œdogonium, Sphæroplea, Chara* and *Vaucheria.* The complexities reported in the formation of auxospores among the diatoms take on new interest in relation to the conditions in *Spirogyra.* In none of these forms have we at present any reason to expect the presence of a sporophytic generation.

Coleochæte has long been regarded as a type of peculiar interest chiefly perhaps because its oospore on germination gives rise to a small group of cells, each of which develops a zoospore. It is not strange that this cellular structure, a phase intercalated between two sexual plants, should have been compared with the simplest types of sporophytes in the liverworts, and that in attempts to bridge the gap between the thallophytes and bryophytes *Coleochæte* should have been brought forward as illustrating the primitive beginnings of a sporophyte generation.

A cytological study by Allen[5] on the germination of the oospore of *Coleochæte,* however, presents evidence that the first mitosis in the oospore is a reduction division and that consequently the later mitoses can not be sporophytic in character. Allen found that when the fusion nucleus made preparations for the first mitosis the chromatic material previously in the form of an irregular network gathered at one side of the nucleus in the manner characteristic of synapsis. There was evidence of a pairing of the chromatic threads during the process of synapsis which is interpreted by this author as indicating a pairing of the chromosomes from the two gamete nuclei. Following synapsis the chromatic material becomes distributed as a coiled thread from which the chromosomes are differentiated, that in a later stage are found scattered through the nuclear cavity. A count of the chromosomes at this stage indicated that the number thirty-two is the double or diploid number for the species studied. Some of the chromosomes were clearly associated in pairs, a condition that becomes more evident in later stages when at metaphase of the first mitosis the now much condensed chromosomes are assembled at the equatorial plate. In this mitosis the chromosomes are short and thick, in sharp contrast to the long narrow bent rods which are characteristic of the second mitosis. Allen then bases his conclusion that the first mitosis in the oospore is a reduction division chiefly on the presence of a stage similar to synapsis preceded by a long resting period, and on peculiarities in the form and grouping of the chromosomes, which peculiarities are similar to those of the heterotypic division in higher plants.

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[5] Allen, C. E., 1905, "Die Keimung der Zygote bei *Coleochæte,*" *Ber. deut. bot. Gesell.,* Vol. XXIII, p. 286, 1905.

It would seem then that *Coleochæte* can no longer be considered as a type very helpful in considerations of the origin of the sporophyte or suggestive of affinities with the archegoniates. With respect to the latter point the simple unicellular character of the sexual organs offers further difficulties to a relationship to the archegoniates, since the multicellular archegonia and antheridia of this last group apparently require an origin from a multicellular type of sexual organ such as is best illustrated among living forms by the plurilocular sporangia and gametangia of the Phaeophyceae. The writer has discussed this problem in a paper on "The Origin of the Archegonium,"[6] and advanced the view that the archegonium and antheridium arose from some type of plurilocular sporangium or gametangium through the differentiation, in response to terrestrial life habits, of a sterile protective envelope around the gametes. Schenck in a contribution "Ueber die Phylogenie der Archegoniaten und der Characeen"[7] accepts the above view and even argues for a direct descent of the archegoniates from the Phæophyceæ, carrying the speculation far beyond the point with which the writer is in agreement. A discussion of the difficulties which face Schenck's hypothesis would, however, lie outside of the province of this paper.[8]

Assuming that the sporophyte is normally characterized by mitoses concerned with the diploid number of chromosomes, the results of the recent research on the Chlorophyceæ make it appear probable that none of the known living types present an alternation of generations even in its simplest form. The striking differences between the Chlorophyceæ and the simplest archegoniates have become more strongly emphasized by the latest research.

Passing to the Phæophyceæ we shall have to consider cytological conditions and life histories very much more complicated than any that are known for the Chlorophyceæ. Only the specialist among the algæ can fully appreciate the diversity of the types and lines of development in the large assemblage of forms termed the brown algæ. The chief groups exhibit greater differences among themselves than do the divergent lines among the green algæ. Unfortunately our information on the cytology of reproduction in the Phæophyceæ is limited to three groups, the Dictyotales, Fucales and Cutleriaceæ, groups which occupy isolated positions of problematical relationship to the lower forms of the Phæophyceæ.

[6] *Ann. of Bot.*, Vol. LXVII, p. 477, 1903.

[7] *Engler's Botan. Jahrbücher*, Vol. XLII, 1908.

[8] See review by Davis, AMER. NAT., Vol. XLIII, p. 107, 1909.

We have from the investigations of Williams[9] an account of the cytology of *Dictyota* throughout the critical phases of its life history. There are three forms of this alga, the male and female sexual plants and an asexual plant which develops spores in groups of four (tetrads) within a tetrasporangium. Earlier research of Mottier indicated clearly that the tetraspore mother-cell is the seat of chromosome reduction, and Williams by studies of the sexual plants as well as the asexual was able to present convincing cytological evidence of an alternation of generations.

Williams found that the sexual plants were characterized by nuclei with sixteen chromosomes and that this number was passed on to the eggs and sperms respectively. Fertilization takes place following the discharge of the gametes, which have the peculiarity of being developed in fortnightly crops, ''each crop being initiated a little before the lowest neap tide, and arriving at maturity about the period of the highest succeeding spring tide''. The motile sperms gather about the eggs which for a short time exert a strong chemotactic influence. Following the union of the gamete nuclei, a second nucleole appears in the fusion nucleus which Williams believes to be the chromatin brought by the sperm. The first mitosis in the egg presents thirty-two chromosomes at the equatorial plate, and this is believed to be the first mitosis of a sporophyte generation represented by the asexual plant and terminating with the development of the tetraspores.

The spindle poles of the first mitosis in the eggs appear to arise by the division of an aster the two poles of which separate until they come to lie on opposite sides of the nucleus. It is an interesting fact that unfertilized eggs begin a parthenogenetic development, but the spindles of the first mitosis are multipolar and the chromosomes are distributed irregularly to a cluster of small nuclei. It would seem then either that the sperm brings to the egg a directive element in the form of an aster, which gives polarity to the fusion nucleus, or that in the absence of fertilization the egg is unable to develop the mechanism necessary for a normal mitosis.

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[9] Williams, J. Lloyd, 1904, ''Studies on the *Dictyotaceæ.*'' I., ''The Cytology of the Tetrasporangium and the Germinating Tetraspore,'' *Ann. of Bot.,* Vol. XVIII, p. 141, 1904. II., ''The Cytology of the Gametophyte Generation,'' *Ann. of Bot.,* Vol. XVIII, p. 183, 1904.

It is the purpose of this paper to consider the nuclear phenomena of sexual reproduction among the algæ in the broadest sense, and this must involve the consideration of any sporophytic generation when present. It has become clearly established by the cytological research of recent years that the sporophytic phase in a life history is a period during which one of the final ends of a sexual nuclear fusion, the intimate association of the sets of parental chromosomes, is delayed and in consequence the mitoses of this period deal with double the number of chromosomes present in the sexual plants. Williams found in the case of *Dictyota* that the mitosis which cuts off the tetraspore mother-cell presented the same large number of chromosomes as the first division of the egg, *i. e.,* twice the number characteristic of the sexual plants. The inference is clear that the vegetative mitoses throughout the development of the asexual plant must be sporophytic in character, and that this generation must have developed from the fertilized egg.

With respect to the two mitoses within the tetrasporangium, the main events are evidently those characteristic of a numerical reduction of the chromosomes. There is a stage of synapsis in which a long thin spirem is found closely coiled in knots against the nuclear membrane. Following this comes a loosening up of the spirem and the differentiation of sixteen chromosomes, the reduced number. The form of the chromosomes, which are loops and closed rings, indicates at once to one familiar with the peculiarities of the heterotypic mitosis that these structures are really pairs of sporophytic chromosomes (bivalent chromosomes) in close association.

The members of each pair are separated by the first mitosis which thus distributes the thirty-two chromosomes in two sets. The second mitosis (homotypic) presents sixteen simple chromosomes in the form of bent rods, similar to those found in the gametophytes. The cytological evidence justifies the conclusion that the tetraspores give rise to the sexual plants and that the fertilized egg must develop the asexual plant, and thus is established an alternation of generations.[10]

The peculiarities of the life history of *Fucus* in relation to the life histories of plants in general are most striking. It became evident from the studies of Strasburger in 1897 and of Farmer and Williams in 1896–98 that the mitoses within the oogonium presented only half the number of chromosomes which were present in the vegetative cells of the Fucus plant. This placed the period of chromosome reduction just previous to the differentiation of the gametes, a condition that is not known in any other group of the thallophytes. To bring such a life history into relation with the prevailing conditions in the lower plants becomes a most interesting problem of plant morphology and phylogeny.

We have recently had from Yamanouchi[11] a much more detailed account of the reduction processes in *Fucus* than the descriptions of the earlier writers. The nucleus within the young oogonium passes through a remarkably clearly defined stage of synapsis during which chromatic threads, derived from a reticulum, become arranged in loops that are gathered together closely attached at one side of nuclear membrane. Close to this point but outside of the nuclear membrane, there is developed an accumulation of kinoplasm from which is differentiated an aster with a chromosome, so that the nucleus during synapsis exhibits strongly marked polarity.

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[10] Since the above was written W. D. Hoyt (*Bot. Gaz.*, Vol. XLIX, p. 55, 1910) has announced his success in raising from the fertilized eggs of *Dictyota dichotoma* fruiting plants which proved to be asexual (tetrasporic) and from the tetraspores sexual plants both male and female. Thus the conclusions based upon cytological evidence have been sustained by cultural studies. Such investigations are especially difficult to conduct in the case of marine algæ, but it is to be hoped that Hoyt's success with *Dictyota* will lead to further studies of this character, especially upon forms of the Rhodophyceæ.

[11] Yamanouchi, S., 1909, "Mitosis in *Fucus*," *Bot. Gaz.*, Vol. XLVII, p. 173, 1909.

The chromatic loops extend into the nuclear cavity and sections show them to be thirty-two in number. After a period of condensation each loop is transformed into a pair of chromosomes by the separation of the arms at the bend. The pairs of chromosomes then become scattered through the nuclear cavity (diakinesis). The interpretation of this history is that the sixty-four somatic chromosomes of the *Fucus* plant are arranged end to end on the spirem and become associated in thirty-two pairs through the formation of the loops. Meanwhile a second aster appears, apparently arising *de novo,* generally at some distance from the first, and the two asters establish the poles of the first spindle. The thirty-two pairs of chromosomes are gathered at the equatorial plate and the members of the pairs distributed in two sets, thus affecting a numerical reduction by one half of the sixty-four somatic chromosomes.

There is apparently no premature division of the chromosomes in preparation for the succeeding division, as is generally the case in the heterotypic mitosis. The second and third divisions in the oogonium are similar in all essentials to typical mitoses. They deal, of course, with thirty-two chromosomes, the haploid number, which divide lengthwise during the metaphase of each mitosis. There is a long period of rest following the second mitosis. The first mitosis in the antheridium is likewise a reduction division similar to that in the oogonium and need not be described in this connection.

The nucleus of the unfertilized egg exhibits no evidence of polarity, but following the entrance of the sperm, according to Yamanouchi, an aster with a centrosome becomes at once evident. A second centrosome with radiations appears later at the point where the sperm fuses with the egg nucleus. These two asters establish the spindle poles of the first mitosis, which presents sixty-four chromosomes. The chromatin of the two gametes is indistinguishable in the fusion nucleus.

The interpretation of the life history of *Fucus* with its phase of chromosome reduction so close to the differentiation of the gametes involves great difficulties. Strasburger has long held the thallus of this plant to be a sporophyte generation, assuming that the gametophyte phase is represented by the third mitosis in the oogonium and the few antheridial mitoses which follow the reduction division. He would then regard the antheridia and oogonia to be derived not from primitive sexual organs, but from sporangia corresponding to the tetrasporangia of *Dictyota*. This view involves a reversal of the relations between the gametophyte and sporophyte generations usual among the algæ, since it supposes the almost complete suppression of the gametophyte. However interesting and suggestive is this interpretation, it can hardly be considered other than a speculation until we know more of the probable phylogeny of the *Fucales*.

It has been evident for a number of years that the life history of the Cutleriaceæ probably involved two phases represented by sexual and asexual plants, respectively, and there has accumulated much evidence from the studies of Reinke, Falkenberg, Sauvageau, Church and others indicating that these phases present a true alternation of generations. The forms most studied have been *Cutleria multifida* with a large much branched thallus which develops gametes, and *Aglaozonia reptans,* a small crustaceous alga which reproduces by zoospores. On the germination of the zygotes and zoospores of these types forms are produced which very shortly take on vegetative characters not of the parent plants, but from the zygotes arise *Aglaozonia*-like sporelings and from the zoospores sporelings totally unlike *Aglaozonia,* but with characteristics of *Cutleria.* Upon this behavior chiefly have been based the suggestions of an alternation of generations in the Cutleriaceæ.

A preliminary paper by Yamanouchi[12] on the above named species presents cytological evidence in support of the theory that they are sexual and asexual phases, respectively, of the same life history, with the relation one to the other of gametophyte and sporophyte. The vegetative mitoses of *Cutleria multifida* and those leading to the formation of the male and female gametes show uniformly twenty-four chromosomes. The zygote develops at once into a sporeling, the nuclei of which have forty-eight chromosomes. There is thus no reduction of the chromosomes at the time of the germination of the zygote, and the sporeling which results must be considered as sporophytic in character.

The vegetative mitoses of *Aglaozonia reptans* exhibits forty-eight chromosomes, but the nuclear divisions within the sporangia are quite different. Following the differentiation of a sporangium, the nucleus passes through a stage of synapsis in which the chromatic spirem is arranged in a series of loops from which are developed twenty-four bivalent chromosomes. The first division in the sporangium is therefore a heterotypic mitosis. Later mitoses in this cell exhibit the reduced number of chromosomes. Since sporogenesis in *Aglaozonia* is accompanied by reduction phenomena, there must be in its life history a sexual phase of which it is the sporophyte generation, and the number of chromosomes as well as other details of cell structure present strong cytological evidence that the gametophyte is *Cutleria*. Such evidence supporting the conclusions of the earlier writers based on the seasonal habits of *Cutleria multifida* and *Aglaozonia reptans* and on the structure of the respective sporelings, makes as strong a case for an alternation of generations in the Cutleriaceæ as is possible short of the actual cultivation of these algæ from zygotes and zoospores to fruiting maturity.

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[12] Yamanouchi, S., 1909, "Cytology of *Cutleria* and *Aglaozonia*," *Bot. Gaz.*, Vol. XLVIII, p. 380, 1909.

These results from studies on the three most highly differentiated groups of the Phæophyceæ (Dictyotales, Fucales and Cutleriaceæ) indicate how complex has been the evolutionary history of the divergent phyla assembled under this name, and how difficult are likely to be the problems of tracing their relationship to lower groups of the brown algæ.

Perhaps in no assemblage of the algæ have the cytological studies of recent date given such striking results as in the Rhodophyceæ. Our understanding of the life history of these forms has been quite revolutionized by the research of three investigators, Wolfe, Yamanouchi and Lewis.

Wolfe[13] from studies on *Nemalion* determined for this type that the sexual organs are not simple uninucleate cells, since the trichogyne possesses a nucleus in addition to that in the carpogonium and the sperm is binucleate and the homologue of the antheridium. The cells of the cystocarp following the fertilization of the carpogonium have nuclei with approximately sixteen chromosomes which is double the number present in the vegetative cells of the parent plant. The cystocarp must then be regarded as sporophytic in character. Because the mitotic figures in advanced stages of the cystocarps showed certain peculiarities Wolfe concluded that a reduction of the chromosomes occurred preliminary to the development of the carpospores. However, he did not trace a process of chromosome reduction through the characteristic phase of synapsis followed by a heterotypic mitosis, and on this point of his investigation more evidence is to be desired. There are certain reasons why in life histories among the Rhodophyceæ of the type of *Nemalion* the process of chromosome reduction may be expected to occur at the time of the germination of the carpospore.

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[13] Wolfe, J. J., 1904, "Cytological Studies on *Nemalion*," *Ann. of Bot.*, Vol. XVIII, p. 608, 1904.

The investigations of Yamanouchi[14] on *Polysiphonia* established the important fact that the carpospore of this form retained the diploid number of chromosomes (forty) present throughout the sporophytic tissue of the cystocarp, and gave rise to a sporeling bearing this number in its nuclei. Furthermore, the tetrasporic plants were found to be diploid in character and the presence of the period of chromosome reduction was established in the tetraspore mother-cell. The nucleus of the tetraspore mother-cell passes through a clearly defined stage of synapsis, following which the forty sporophytic chromosomes are found associated in twenty pairs (bivalent chromosomes). The first mitosis distributes the members of these pairs and is therefore a reduction division. The tetraspore has then the haploid number of chromosomes (twenty) and on germination develops a sporeling with this reduced number, which was found to be characteristic of the sexual plants. It is reasonable to conclude that in the life history of *Polysiphonia* the sexual plants alternate with the tetrasporic, each phase arising from the spores produced upon the other. Yamanouchi expressed the belief that "the sexual plants and tetrasporic plants present two distinct phases of an antithetic alternation of generations, with the cystocarp a part of the sporophytic phase".

The many interesting points in the history of the development of the sexual organs and the cystocarps are too detailed to be presented in this brief review. Yamanouchi, however, supports Wolfe's conclusion that the trichogyne in early stages of development contains a nucleus, and that the sperm is the homologue of an antheridium, although in *Polysiphonia* this cell is uninuculeate. Some criticisms of Kurssanow[15] on the work of Wolfe upon these latter points must also be omitted.

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[14] Yamanouchi, S., 1906, "The Life History of *Polysiphonia*," *Bot. Gaz.*, XLII, p. 401, 1906.

[15] *Flora*, Vol. XCIX, p. 111, 1909.

A detailed study by Lewis[16] of the life history of *Griffithsia* is in agreement with the results of Yamanouchi on the essential facts of an alternation of sexual and tetrasporic plants and the behavior of the chromosomes throughout the various phases of the similar life histories. The sexual plants have seven chromosomes, the haploid number. The cystocarp presents nuclei with fourteen chromosomes and is clearly a sporophytic phase which, as in *Polysiphonia,* develops with the cooperation of the cytoplasm in certain cells of the gametophyte; the carpospores have fourteen chromosomes. The tetrasporic plants are characterized by fourteen chromosomes, the diploid number, and may be assumed to arise from the carpospores. The first mitosis in the tetraspore mother-cell is a reduction division preceded by the characteristic stage of synapsis from which the chromosomes emerge in seven pairs. Seven chromosomes, therefore, pass to the tetraspores from which the sexual plants may be expected to develop.

It is known that in a number of species of red algæ structures resembling tetraspores are occasionally found on sexual plants and that procarps are sometimes present on tetrasporic individuals. Such conditions, first observed by Bornet, have more recently been noted by Lotsy for *Chylocladia kaliformis,* Yamanouchi for *Polysiphonia violacea,* Lewis for *Griffithsia Bornetiana,* and by the writer for *Spermothamnion Turneri, Callithamnion Baileyi* and *Ceramium pedicillatum.* Furthermore, certain of the red algæ, as *Rhodymenia palmata* on the New England coast, present tetrasporic plants in great abundance, while cystocarpic individuals are rare or unknown. Certain critics see in the above phenomena serious difficulties for the theory of alternation of generations in the Rhodophyceæ so strongly supported by the work of Yamanouchi and Lewis.

These authors had only limited material of what seemed to be tetraspore mother-cells on sexual plants, but in this material the apparent tetrasporangia failed to mature tetraspores, the cleavage furrows proceeding only a short distance into the mother cells while the nuclei either remained undivided (*Polysiphonia*) or produced groups of several nuclei (*Griffithsia*). Thus such cytological evidence as we have on these irregularities indicates them to be abnormal developments. Examples of apogamy and apospory are now recognized as by no means uncommon in the higher groups of plants exhibiting alternation of generations, and it will not be at all surprising if such phenomena or related irregularities of life history are found among the Rhodophyceæ. Such peculiarities must of course be thoroughly studied to determine whether or not they will prove to be the exceptions that support the rule. The investigations of recent years on apogamy and apospory in the pteridophytes have in no way weakened the acknowledged alternation of generations in that group.

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[16] Lewis, I. F., 1909, "The Life History of *Griffithsia Bornetiana,*" *Ann. of Bot.,* Vol. XXIII, p. 639, 1909.

A very interesting problem is presented in the phenomenon described by Osterhout[17] of the germination of the tetraspores of *Agardhiella tenera* (*Rhabdonia tenera*) while still imbedded in the tissue of the parent plant. A peculiarity of this development is the behavior of the group of tetraspores as a unit, so that all four cells enter into the formation of a sporeling. It is important to note that the sporelings are very commonly sexual plants, as would be expected from the germination of normal tetraspores. It seems quite possible that the occasional tetrasporic shoots reported by this author are products of a tetraspore mother-cell in which the reduction mitoses have been suppressed, and therefore the tetrasporangium, behaving like a monospore, would naturally give rise to a tetrasporic plant. This is a problem which should be investigated, because if the above suggestion prove true, this behavior of the tetraspores of *Agardhiella* would present strong evidence in support of the theory of alternation of generations in the Rhodophyceæ. The peculiarity of *Rhodymenia palmata* on the New England coast, referred to above, may likewise rest upon a suppression of reduction phenomena in the tetrasporangium which would lead to the omission of the sexual phase from the life history and permit of an indefinite succession of tetrasporic plants.

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[17] Osterhout, W. J. V., 1896, "Life History of *Rhabdonia tenera* J. Ag.," *Ann. of Bot.*, Vol. X, p. 403, 1896.

It is very important that the life histories of some of the simpler red algæ be investigated, especially such forms as have *Chantransia*-like stages characterized by the production of monospores. The fact that the reduction divisions of *Polysiphonia* and *Griffithsia* are not associated with the formation of carpospores leads one to suspect that the period of chromosome reduction in such types as *Batrachospermum* and *Nemalion* may occur at the time of the germination of the carpospore. Should this prove to be the case, the origin of the tetrasporic phase, characteristic of the higher Rhodophyceæ, may without difficulty be conceived as the result of a postponement of the reduction divisions and their association with a type of cell similar to and perhaps identical with a monosporangium. Such a postponement or delay in the expression of the reduction divisions would establish at once a plant with the diploid number of chromosomes (tetrasporic plant) and introduce into the life cycle the tetrasporangium as a new type of reproductive organ.

Lewis regards the tetrasporic plant as illustrative of ''an homologous alternation of generations, not the equivalent, wholly or in part, of the sporophyte of the archegoniates'', and he thereby limits the sporophytic phase in the life history to the sporogenous cells of the cystocarp. This conclusion is based on the morphological resemblance of the tetrasporic plants to the sexual, although Lewis himself points out important differences between the two. Thus ''tetrasporic plants (of *Griffithsia Bornetiana*) are always more abundant, as well as on the average larger than sexual plants" a condition which is true of a number of species of the Rhodophyceæ with which the writer has had a rather extensive field acquaintance. This is a point of some importance, since too great emphasis may be placed on the resemblance in form between the two generations (a resemblance which seems most natural since the plants develop under closely similar life conditions), and important differences in size, dimensions of the cells, and general vegetative vigor may not receive the attention that they deserve. If the fusion of gamete nuclei is to be regarded as the stimulus to a sporophytic generation, the period of chromosome reduction is equally characteristic of its end, and the second event follows as a natural consequence upon the first. Mitoses with the diploid number of chromosomes whenever they occur between these two events furnish, in the opinion of the writer, the only safe criteria of the extent and duration of a sporophytic generation in normal life histories.

Yet it has become clear from recent research on apogamy and apospory that the mere number of chromosomes, whether haploid or diploid, does not determine the morphology of the generation, gametophyte or sporophyte, with which they are associated. The reasonableness of this principle is apparent when regarded from another point of view. The inheritance which is responsible for the development in a type of a sporophyte generation must be carried by the sexual phase, and the potentialities of a sexual generation must be present in the sporophyte, although in normal life histories the inheritance is latent at certain stages and only becomes operative in both generations after definite periods of development have been passed. The two germ cells, eggs and spores, do not give rise to different generations because they expressly contain a single or a double set of the chromosomes characteristic of the species; the causes of their respective developments are too complicated to be expressed in such simple terms.

To the writer the differences between the egg and the spore appear to be such as may depend primarily on a greater vigor and vitality given to the egg by the fusion of the gametes, a vigor which has expressed itself in such varied morphological manifestations because of the different conditions under which the sporophyte generations have become established in the numerous phyla characterized by their presence. The conditions affecting the sporophyte are not alone those of physical environment; there are also those evolutionary factors that operate to adjust the plant, as far as is possible, to its place among other organisms. One conclusion stands out clearly among the difficulties of these problems: as in the case of sex, the sporophyte has probably arisen independently a number of times in the evolution of plants.

So we are brought to the end of our discussion of the nuclear phenomena of sexual reproduction in the algæ to the problems of the origin of the sporophyte and the relations of the sexual and asexual generations to one another, whether or not they are essentially homologous or antithetic in the alternation of generations. It is not the purpose of this symposium to consider these matters, but allusions and inferences could not be kept out where the vital connections between the subjects under consideration and these larger speculations are so close. The immediate need of such discussion is perhaps not so great for the reason that the pages of the *New Phytologist* for 1909 have presented two important papers of Lang and Blackman representing the opposite schools together with a report of a discussion in which a number of the leading British botanists took part. That the writer's sympathies are strongly with the hypothesis of antithetic alternation of generations must have been apparent from the tenor of this paper.

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